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Tree cover and biomass increase in a southern African savanna despite growing elephant population

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Abstract. The growing elephant populations in many parts of southern Africa raise concerns of a detrimental loss of trees, resulting in overall reduction of biodiversity and ecosystem functioning. Elephant distribution and density can be steered through artificial water points (AWPs). However, this leaves resident vegetation no relief during dry seasons. We studied how the introduction of eight AWPs in 1996 affected the spatiotemporal tree-structure dynamics in central Chobe National Park, an unfenced savanna area in northern Botswana with a dry-season elephant density of ;3.34 individuals per square kilometer. We hypothesized that the impact of these AWPs amplified over time and expanded in space, resulting in a decrease in average tree density, tree height, and canopy volume. We measured height and canopy dimensions of all woody plants around eight artificial and two seasonal water points for 172 plots in 1997, 2000, and 2008. Plots, consisting of 50 3 2 m transects for small trees (0.20–3.00 m tall) nested within 50 3 20 m transects for large trees (≥3.0 m tall), were located at 100, 500, 1000, 2000, and 5000 m distance classes. A repeated-measures mixed effect model showed that tree density, cover, and volume had increased over time throughout the area, caused by a combination of an increase of trees in lower size classes and a decrease in larger size classes. Our results indicate that the decrease of large trees can be attributed to a growing elephant population. Decrease or loss of particular tree size classes may have been caused by a loss of browser-preferred species while facilitating the competitiveness of less preferred species. In spite of 12 years of artificial water supply and an annual elephant population growth of 6%, we found no evidence that the eight AWPs had a negative effect on tree biomass or tree structure. The decreasing large-tree component could be a remainder of a depleted but currently restoring elephant population.

INTRODUCTION

The African elephant (Loxodonta africana Blumenbach) is one of the few animal species capable of transforming entire woodland ecosystems into open grassland or shrubland (Owen-Smith 2002). Excessive hunting pressure in the late 19th century led to a decimation of elephant populations in southern Africa (Campbell 1995). The African elephant was listed in the CITES Appendix I in 1989 (Blanc et al. 2007). Since then, successful conservation measures have resulted in significant restoration of elephant populations, especially in southern African countries. As local elephant populations continue to grow at an increase of ~5% per annum, ecologists and wildlife managers are increasingly confronted with elephant-induced ecosystem changes (Hoare 1999, Baxter and Getz 2005, Van Aarde and Jackson 2007; see Plate 1).

An effective means to manipulate the spatiotemporal distribution of water-dependent species is through the provision of artificial watering points (AWPs; Chamaille ´-Jammes et al. 2007). The establishment of AWPs, however, is controversial as year-round presence of animals could lead to artificially inflated and prolonged browsing pressure in otherwise water-

limited areas (Smit et al. 2007a). Indeed, the decrease of the large-tree vegetation component in the Kruger National Park (South Africa) has been attributed to increased elephant densities as a consequence of the large number of AWPs here. Sequential photography revealed that the density of trees >5 m decreased in the Kruger Park by up to 38% on basalt-derived soils within a 12-year study period (Eckhardt et al. 2000). While the authors of this study were cautious to attribute the observed tree density decrease to the growing elephant population alone, they suggested the closing of AWPs as a possible management measure to be taken, should large-tree density further decrease. However, in Hwange National Park (Zimbabwe) an aerial photograph analysis failed to detect sizable changes in woody vegetation cover over a 16-year study period, in spite of exponentially increasing elephant numbers in the area (Valeix et al. 2007).

The largest free-ranging elephant population of Africa, with an estimated population size of ~200 000 elephants, is found in the recently proclaimed Kavango- Zambezi Transfrontier Conservation area, an area of >300 000 km^2, straddling national borders of Angola, Botswana, Namibia, Zambia, and Zimbabwe (Van Aarde and Jackson 2007). The 2006 census showed that of these animals ~40 767 mostly resided in Chobe National Park and its surroundings (Blanc et al. 2007). During the wet season, when water is abundantly available in natural seasonal pans, this large population of elephants becomes scattered throughout the area. During the dry season the large herds congregate around the few available water sources, and thereby change vegetation structure, through coppicing and thinning, particularly affecting the fringes of the Chobe River (Mosugelo et al. 2002, Moe et al. 2009). Outside the riparian zone of the Chobe River, however, woody vegetation remains largely unaffected by increasing elephant numbers (Skarpe et al. 2004).

In an attempt to reduce elephant browsing pressure along the Chobe River, the Chobe Park management has been systematically providing water through eight AWPs since 1996 (C. Winterbach, personal observation) in the Nogatsaa area of Chobe National Park (~80 km south of the Chobe River front; see Fig. 1). Establishment of these AWPs transformed this area from waterlimited to food-limited for water-dependent animals (Andrew 1988, Chamaille´ -Jammes et al. 2007). Increased and year-round browsing pressure, particularly from elephants, is expected to reduce tree density and height within the influence zones of these AWPs (Ben- Shahar 1993, Brits et al. 2002). No significant changes were found in the vegetation composition or biomass within the first three years after the AWPs were made operational (Winterbach and Kalwij 2000). However, the elephant population of Chobe has been continuously growing at a ~6% rate (Gibson et al. 1998, Blanc et al. 2007). We therefore predict that elephants will ultimately affect the ecosystem around the AWPs (Hiscocks 1999, Calenge et al. 2002, but see Valeix et al. 2007).

This study evaluated how spatiotemporal patterns in savanna tree structure were affected by the first 12 years of systematic provision of artificial water to animals. We hypothesize that this supply of water led to a decrease in height, density, cover, and canopy volume of trees in savanna woodlands around the AWPs, as a result of year-round browsing within the influence zone of these waterpoints. We tested this hypothesis by counting and measuring canopy dimension of trees (>0.20 m in height) around AWPs and seasonal pans in 1997, 2000, and in 2008.

MATERIALS AND METHODS

Study area

The study area is located in the Nogatsaa section of Chobe National Park, Botswana (24°49´–25°07´ E, 18°06–28´ S; see Fig. 1). It is a relatively flat area at an altitude of ~1000 m. Vegetation in this region is described as woodlands dominated by Baikiaea plurijuga and various species of Combretum on deep Kalahari sands, Colophospermum mopane-dominated savanna on basaltic soils, and edaphic grasslands on lacustrine soils (Child 1968). Climate is semiarid with a highly variable mean annual precipitation ranging from 550 mm in the southwest to 680 mm in the northeast of the Park, mainly falling from October to April (Department of Wildlife and National Parks 2001). The nearest permanent water source is the Chobe River flowing 50 km north of the Nogatsaa area, forming the northern boundary of the Park and the political border between Botswana and Namibia.

The Nogatsaa area is characterized by a complex of heterogeneously distributed natural seasonal pans and eight AWPs (located on formerly seasonal pans) in an area spanning 30 x 40 km. Prior to the introduction of these AWPs, the distance of >50 km from permanent water (Chobe River) prevented elephants from residing here throughout the year, as remoteness from drinking water exceeds ranging behavior of elephants (Stokke and du Toit 2002). The boreholes of these AWPs were drilled in 1967 (Deloitte and Touche 1992), but it was not until 1996 that water was systematically provided (C. Winterbach, personal observation).

Seasonally migrating, free-ranging elephants have been observed in the area since 1945 onward only (Child 1968). Until 1996, long-distance roaming, depending on water availability, was a natural behavioral feature of this elephant population (Verlinden and Gavor 1998). The artificial water supply changed behavioral patterns by enabling elephants to reside in the AWPs area throughout the year (Gibson et al. 1998).

Sampling design

We collected data in 138 plots immediately after the artificial water supply commenced around eight AWPs during the months April–June in 1997, 2000, and in 2008 (Fig. 1). An additional 34 plots were sampled around two seasonal pans as control in 2000 and in 2008. The seseasonal pans were located at respective distances of 11 and 17 km from the nearest AWP. A total of 172 plots were thus located in the four cardinal directions around waterpoints at 100, 500, 1000, 2000, and 5000 m distance, if inter-waterpoint distances permitted. We located the exact position of previous plots by using a handheld GPS (Garmin 12XL; Garmin, Olathe, Kansas, USA) in combination with field photos taken in 1997 and/or in 2000. This method proved to be very successful as we were able to locate nearly all 172 plots; only five plots were located using merely the GPS position due to lack of photos or adequate reference landmarks.

Tree measurements

We measured tree height and canopy of individual trees by following the BECVOL method (Smit 1996). This method uses seven measurements to calculate canopy volume for each tree: (1) tree height, (2) height of maximum canopy diameter, (3) height of first leaves or potential leaf-bearing branches, (4 and 5) maximum canopy width in two perpendicular directions, and (6 and 7) base width of the foliage in two perpendicular directions at height of first leaves. Tree dimensions were measured at 0.05-m intervals.

Each plot consisted of a 50 x 2 m small-tree transect for all woody plants of 0.20–3.00 m in height, nested within a 50 x 20 m large-tree transect for woody plants ≥3.00 m. If the number of trees per transect was <10 trees, those transects were extended in length and/or

width, up to a maximum of 200 x 2 m for small-tree and 200 x 200 m for large-tree transects, respectively.

Tree density, canopy volume, and canopy cover were standardized to density *d* in number of trees per hectare, canopy volume *v* in m^3/m^2, and canopy cover *c* in m^2/m^2, respectively. Average height of trees in small-tree and large-tree transects was analyzed separately; tree heights (small, h_s; large, h_l) are expressed in meters for small-tree and large-tree transects, respectively.

We fitted linear mixed-effect models to the response variables tree density, canopy cover, canopy volume, and tree heights (h_s and h_l) to determine if supply of artificial water to animals had an effect on spatiotemporal tree dynamics. In contrast to a general linear model, linear mixed-effect models have the advantage of efficiently handling missing values and unbalanced designs, accommodating multiple error terms, and defining the correlation structure of the error terms (Piepho et al. 2004).

We analyzed our observational setup as a repeatedmeasures split-plot design (Quinn and Keough 2002), where the factors treatment (seasonal pans vs. artificial water supply) and distance from waterhole (100, 500, 1000, 2000, and 5000 m) were considered as fixed variables while the factors waterhole and direction nested within waterhole were treated as random block variables. Time, expressed as year of observation (1997, 2000, and 2008), was considered as a within-subject effect between plots, allowing us to distinguish between the degree of variation across time for each plot (withinplot change), and the variation among plots (betweenplot change) (Pinheiro and Bates 2000). Because the within-plot residuals are not independent, and they are expected to vary between plots, we applied a first-order autoregression covariance structure to our models, using plot as a random variable. We thus tested the general model $Y_{ijk}=X_{ijk} + waterpoint_i + direction_{ij}(waterpoint_i) + plot_{ijk}$ where *i* denotes the waterpoint, *j* the direction within waterpoint *i*, and *k* the repeated observation for plot *k* (Piepho et al. 2004). Explanatory variable or variables X_{ijk} consisted of treatment, time, distance from waterpoint, or a combination of these three variables as indicated in Table 1. The best-fitting model was selected based on lowest Akaike's Information Criterion (AIC) values under the restriction that each explanatory variable contributes significantly at the $P < 0.05$ level.

Both canopy volume and canopy cover were squareroot transformed to satisfy the assumption of normality, while tree height h_s and h_l were natural log-transformed (Quinn and Keough 2002). At the tree level Wilcoxon two-sample tests were used to determine if and how the height distribution of individual trees differed between treatments and years. Finally, we calculated the Gini coefficient G_s and G_l for small and large-tree plots, respectively, as a quantification of tree size inequality (Weiner and Solbrig 1984). Values, calculated from tree height and rank numbers, vary between 0 and 1, whereby 0 indicates perfect equality of tree size distribution and 1 indicates perfect inequality, i.e., all trees but one are of the same size. This coefficient is used to assess temporal changes in length–frequency distributions and has the advantage that it allows comparison of highly variable populations (Weiner and Solbrig 1984). All statistical analyses were conducted in SPSS 16.0 (SPSS 2007).

RESULTS

Neither the supply of artificial water nor distance from AWPs could explain the differences in tree densities (Table 1). The best-fit model indicated that the increase of tree density over time was significant (P_{Year}, <0.001). This increase was most prominent at the 100- and 500-m plots around the seasonal pans (Fig. 2). We measured an initial decrease in tree density around AWPs between 1997 and 2000, but overall density increased significantly between 1997 and 2008. This increase can largely be attributed to an increase of trees in the 0.20–3.00 m category, while trees of the larger size classes decreased. Because no significant interaction

effects were found, the model with time as main effect only was considered the best fitting model.

The variation in canopy cover was also only explained by time (Table 1). We found no significant interactions between any of the main factors (all $P > 0.05$), hence the main-effects model with time as a sole variable was regarded as the best fitting model. In fact canopy cover almost doubled during the period 1997–2008 in plots, both around seasonal pans and AWPs alike (Fig. 2). The relative contribution of large trees (≥3 m) was much larger for cover than tree density, which also explains the larger variation in overall canopy cover.

Time was also the best predictor for canopy volume, a derivate from, among others, canopy cover and tree density (Table 1), although the impact of time was not as strong as that observed for canopy cover. Large trees made up the greater part of canopy volume, but the increase of canopy volume over time was mostly attributable to the increase of small-tree canopy volume (Fig. 2).

Tree height of small and large trees, h_s and h_l respectively, were both best explained by a combination of time and treatment nested within time (Table 1). Average tree height, however, only differed significantly between treatments for large trees (>3.0 m; P = 0.040), where average large-tree size showed a decrease between 1997 and 2008 to the level of that of large-tree transects around seasonal pans in 2008 (Fig. 3). No such trend was observed for small trees, nor was there an effect of distance from AWPs on the rate of decline (Table 1; P= 0.478).

A breakdown of the individual tree height distribution at the various distances for both treatments showed that small and large trees responded differently over time. The proportion of trees in the higher tree size classes (>10 m) strongly decreased or disappeared entirely between 1997 and 2008, while trees of the lower size classes either persisted or increased in their proportional presence (Fig. 4). This shift in tree size class distribution was almost exclusively observed in plots around AWPs, while little to no change was observed around the seasonal pans, as confirmed by the Wilcoxon twosample rank tests (Table 2). These tests also show that the difference in the tree size class distribution between seasonal pans and AWPs gradually decreased over time.

The Gini coefficients confirmed the significant effect of time for both small- and large-tree transects (for small trees, P=0.001; for large trees, P < 0.0001), while there was no significant difference in Gini coefficients between seasonal pans and AWPs (both P > 0.05). In the smalltree transects, inequality increased over time around seasonal pans but not so around AWPs (Fig. 5). For large-tree transects, however, tree size inequality de creased around both seasonal pans and AWPs, though this decrease was strongest around the former, indicating a loss of large trees. No effects of distance from waterpoints could be detected for either value of the Gini coefficients.

DISCUSSION

To the best of our knowledge this is the first study comparing vegetation structure dynamics around seasonal pans and AWPs that included baseline data from soon after the opening of AWPs (sensu Brits et al. 2002). After 12 years of providing drinking water to waterdependent animals, we found a clear increase of tree density, cover, and canopy volume. This increase, however, was not limited to the 2–5 km radius around AWPs as the rates of increase were approximately the same around seasonal pans and AWPs alike. Moreover, decrease both in height and number of large trees (≥3.0 tall) was also unrelated to AWPs. Both trends, therefore, suggest that the first 12-year period of water provision has had no measurable effect on vegetation structure dynamics within the immediate influence zones of the AWPs. These findings are in contrast with the general assumption, and our hypothesis, that water provision leads to a decrease of tree density, browse availability, and/or tree height in the influence

range of AWPs due to year-round browsing pressure (see, for instance, Brits et al. 2002, Chamaille´-Jammes et al. 2007, Smit et al. 2007a, Holdo et al. 2009).

Availability of permanent water allows water-dependent animals to reside in an area throughout the year, leading to a high impact on vegetation in the immediate vicinity of waterpoints (Owen-Smith 2002, Shannon et al. 2006, Smit et al. 2007a). For example, in Kruger National Park (0.63 elephants/km2; Blanc et al. 2007) tree density is close to zero in the first 100 m, and subsequently increases up to a distance of 2.8 km from AWPs (Thrash 1998, Brits et al. 2002). In Chobe National Park (3.34 elephants/km^2; Blanc et al. 2007) the conversion of >30% of the woodland vegetation into shrubland between 1963 and 1998 has been attributed to the strong increase of elephant browsing pressure along the Chobe River (Mosugelo et al. 2002). In contrast to our hypothesis we found no relationship between any of the vegetation structure variables and distance from water, not even for the 100-m plots.

Elephants are water-dependent animals and usually do not roam beyond a distance of 3–6 km from permanent water during the dry season (Stokke and du Toit 2002, Leggett 2006). However, elephants exhibit sexual dimorphism in their spatial distribution, especially during the dry season (Smit et al. 2007b). While calf-caring herds roam within close proximity to permanent water, bulls are known to cover much larger distances. Indeed, independently ranging elephant bulls have been readily observed to browse at distances >10 km from water (Stokke and du Toit 2002, Shannon et al. 2006, Chamaille´-Jammes et al. 2007). Also the feeding behavior of elephant bulls differs from that of cows, whereby bulls are more destructive, targeting taller trees, while cows show a preference for smaller trees (Styles and Skinner 1997, 2000, Shannon et al. 2008). Indeed, the observed decrease in numbers of large trees (Fig. 4) is possibly caused by elephant impact. More importantly, elephants were virtually absent from central Chobe prior to 1945 (Child 1968). This absence could have created a window of opportunity for large trees to build up into high numbers (Skarpe et al. 2004). The current decrease of large trees could thus be an ecosystem response to an increase in elephant densities. Long-term experimental enclosures could be established to quantify this response, but is impracticable due to the remoteness of this area.

Elephant-preferred tree species, such as Colophospermum mopane or various species of Combretum, can regenerate by coppicing in response to browsing (Smallie and O'Connor 2000). Such browsing of trees can lead to an accelerated growth for certain species, or even to increased browse availability after regrowth (Rutina et al. 2005). Moreover, gaps may be created in which quicker growing tree species may establish (Baxter and Getz 2005). Browsing-related tree growth responses could therefore be the ecological mechanism behind the increase of trees in the lower size classes (Smallie and O'Connor 2000, Fornara and du Toit 2007). However, about one-third of the study area, mainly located in the northern section of the study area, consisted of Baikiaea plurijuga-dominated vegetation, a vegetation type that elephants tend to avoid due to the unpalatability of the dominant species (Holdo 2007). Elephant browsing alone may therefore not be the only factor explaining the decrease of large trees.

Fire has been proposed as the other major cause of large-tree loss and shrub encroachment in the woodland dynamics of northern Botswana (Ben-Shahar 1996a, 1998). Many dead standing large trees, present in the 1997 field photos, were found fallen over in 2008. Most of these dead trees showed clear marks of recent fire events (J. M. Kalwij, personal observation). Indeed, a man-made fire occurred in the northern part of the study area in 2005 (Botswana Department of Forestry, unpublished data). The impact of fires strongly depends on the time of burning and on the vegetation type (Ben- Shahar 1996a). While mopane woodlands readily resprout, Baikiaea plurijuga-dominated vegetation is prone to fire damage, and the large-tree component may disappear entirely (Childes and Walker 1987,

Ben- Shahar 1998). Fire may therefore have contributed to the loss of large trees in the Baikiaea woodlands in the northern part of the study area.

A lack of woodland regeneration, and a subsequent loss of biodiversity, is a major concern in elephantdominated protected areas (Shannon et al. 2008). A 20- year experiment, for example, showed that elephants were capable of preventing woodland regeneration (Western and Maitumo 2004). Decline of elephant preferred species has been attributed to a high elephant browsing intensity (Shannon et al. 2008). However, stochastic events such as fire or dry–wet cycles can equally affect woodland regeneration by either suppressing or triggering seedling establishment (Prins and Van Der Jeugd 1993, Ben-Shahar 1996b, Sankaran et al. 2005). Furthermore, bush encroachment can also occur when elephant browsing pressure is low due to a release from browsing (Prins and Van Der Jeugd 1992). Such events could have especially affected the density of the small-tree size classes, increasing the inequality in tree size distribution. Still, we found no tree size class or tree structure inequality suggesting that stochastic events or a high elephant impact affected tree recruitment (Fig. 5).

A cycle of dry years (drought) can greatly contribute to the reduction of tree density and decrease of canopy volume (Ben-Shahar 1996b, Van Langevelde et al. 2003). During the first half of the 20th century and in the early 1990s, northern Chobe experienced a cycle of dry years and increased occurrence of bushfires (Botswana Department of Forestry, unpublished data; Barnes 2001, Mazvimavi and Wolski 2006). Indeed, elephant diet selection and seasonal movement are correlated with rainfall with elephants increasingly relying on woody vegetation during periods of drought (Cerling et al. 2009). More recently, however, several wet years occurred between 2004 and 2008 (Botswana Weather Bureau, unpublished data). Furthermore, increased availability of surface water in the seasonal pans could have reduced the length and intensity of browsing pressure around the AWPs (Chamaille´-Jammes et al. 2007). The series of wet years that northern Botswana is currently experiencing could therefore have contributed to the increase of tree density, cover, and canopy volume due to a reduction of small-tree mortality on the one hand, and an increased tree recruitment on the other.

Conclusions

We found no evidence supporting the hypothesis that the first 12 years of supplying water to animals has had an unsustainable effect on tree density and/or tree biomass in central Chobe. In spite of a growing elephant population, tree density, canopy cover, and volume increased throughout the area. We suggest that these increases were mainly caused by a combination of duration and location of fire events, and a recent series of wet years, while the loss of large trees was due to increasing elephant numbers. This combination of factors affected the entire area rather than localized zones around AWPs.

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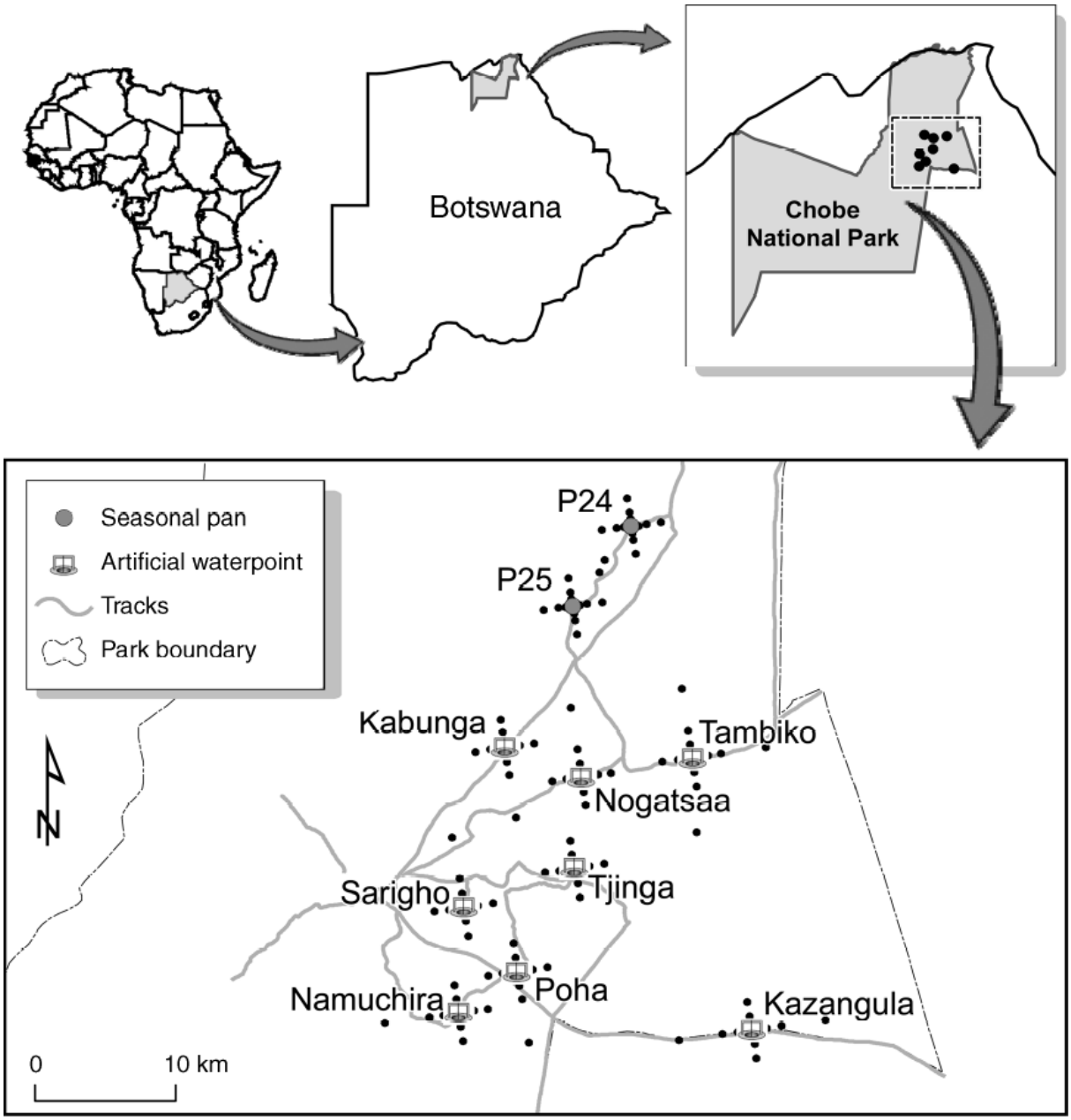
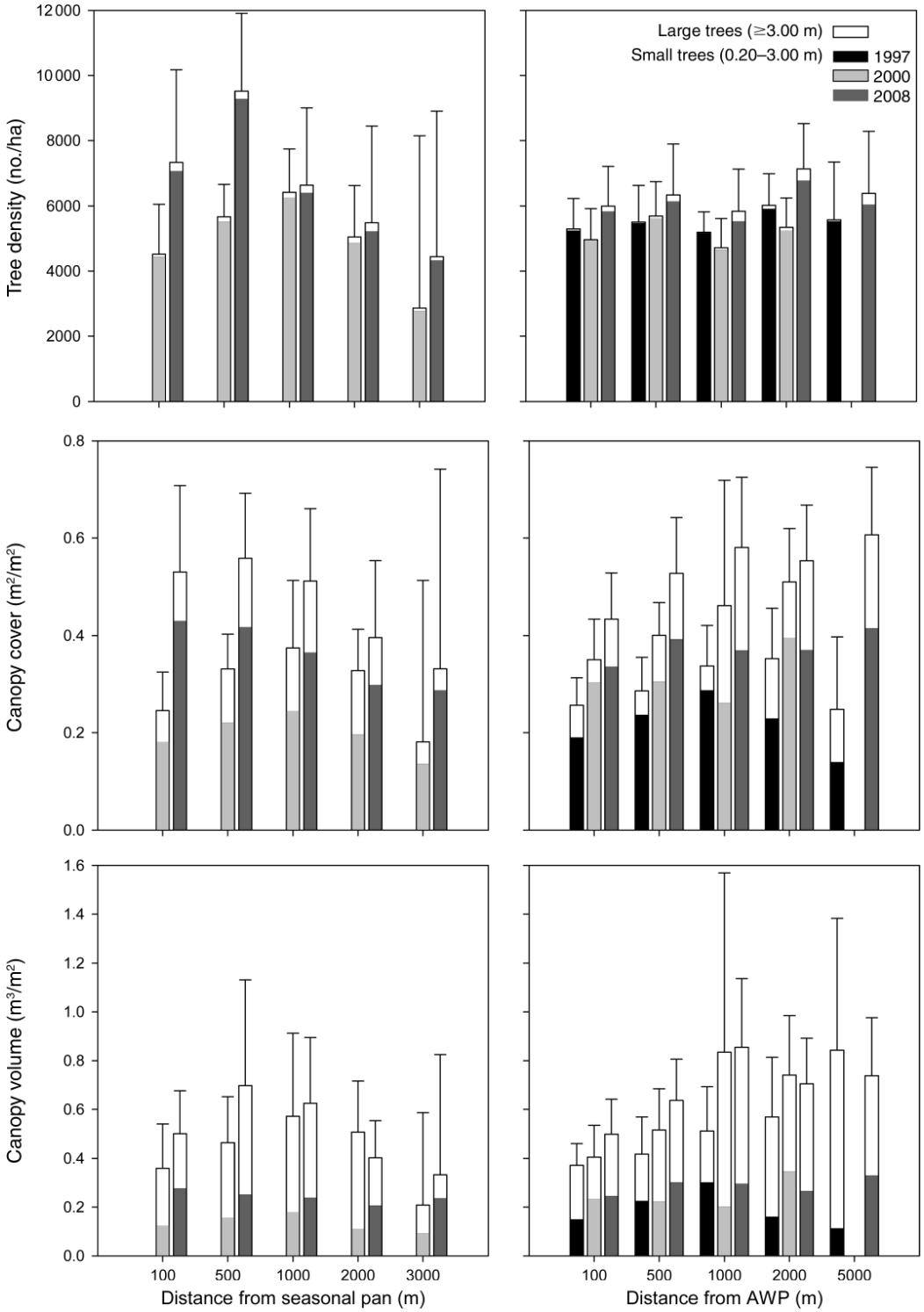
FIG. 1



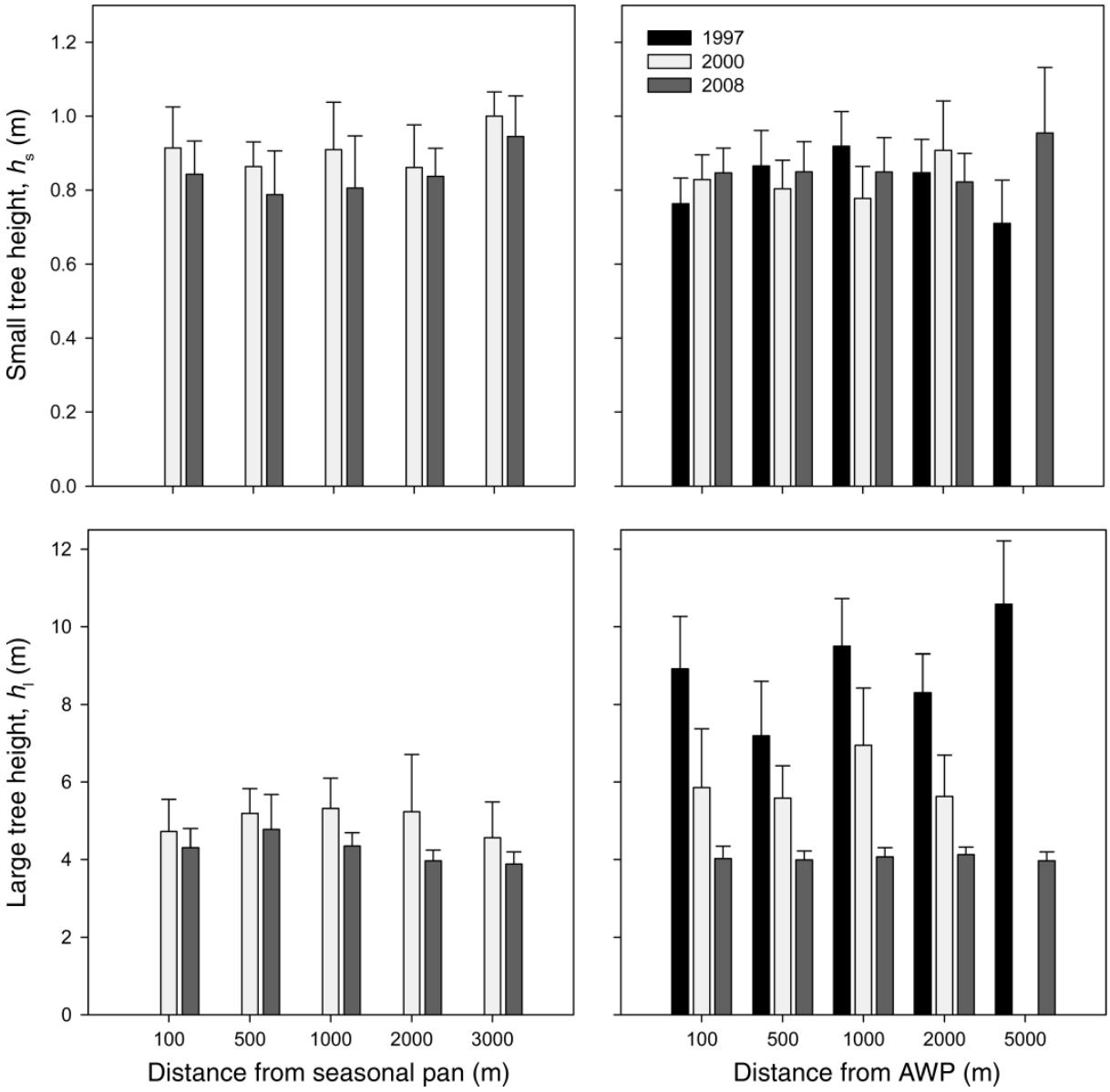
Location of the Nogatsaa area in central Chobe National Park, Botswana. The lower panel illustrates the position of the eight AWPs (artificial waterpoints) and two reference seasonal pans; positions of the sample plots (N¼172) are also shown by the small solid circles. FIG. 1. Location of the Nogatsaa area in central Chobe National Park, Botswana. The lower panel illustrates the position of the eight AWPs (artificial waterpoints) and two reference seasonal pans; positions of the sample plots (N¼172) are also shown by the small solid circles.

FIG. 2.



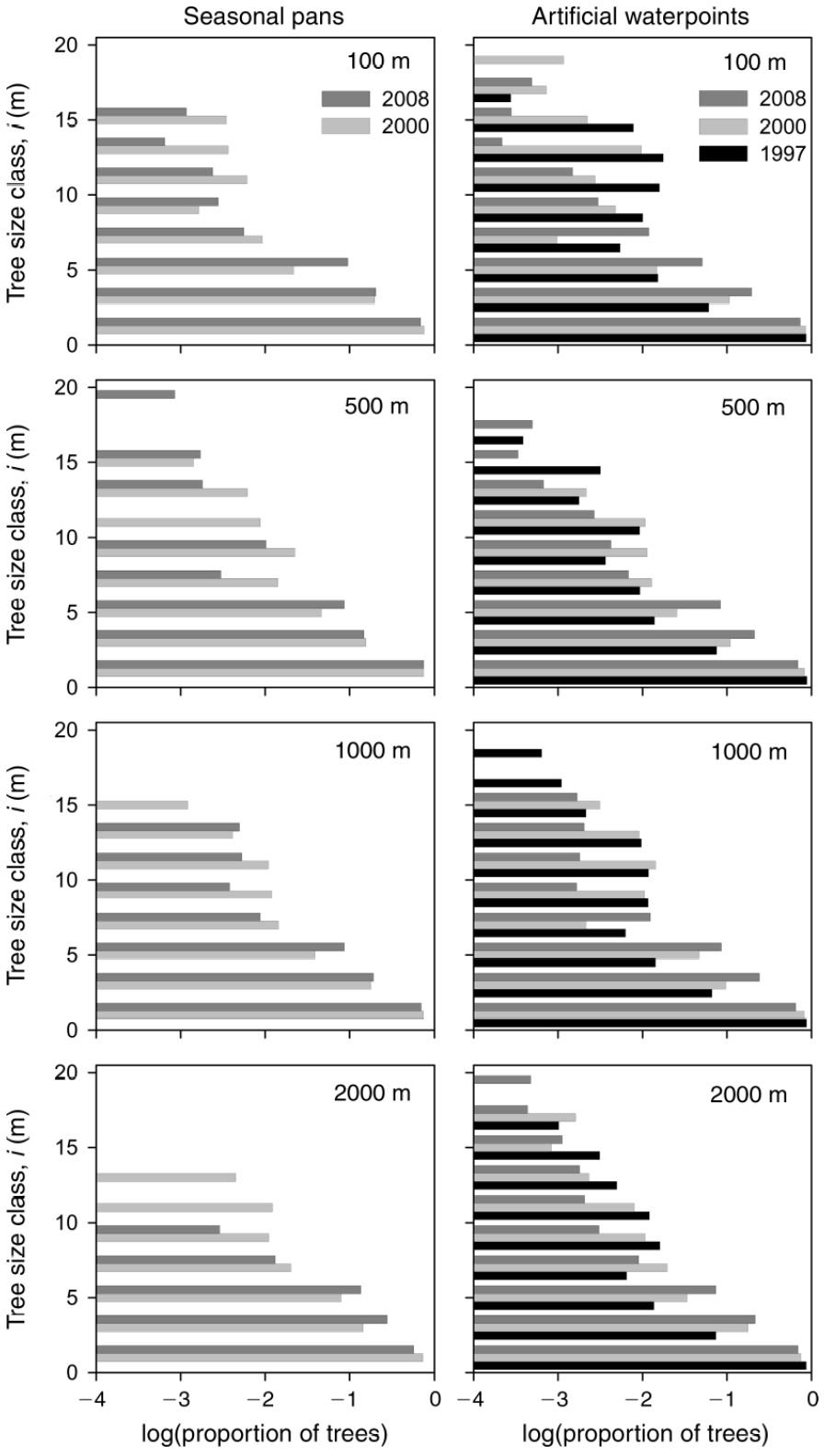
Changes over time in average tree density, relative canopy cover, and relative canopy volume (means and 95% confidence interval) for each distance category around seasonal pans and AWPs. The large-tree transect contribution to the total values is highlighted by the open part of the bars, while the solid sections of the bars indicate the contribution of small-tree transects for each respective sampling year. Large-tree transects were sampled simultaneously with small-tree transects.

FIG. 3.



Changes over time in average tree height for each distance category around seasonal pans and AWPs for small trees and large trees in different sample years. Axis values are mean and 95% confidence interval.

FIG. 4.



Changes over time in average tree height distribution at plot level for distance categories 100, 500, 1000, and 2000 m around seasonal pans and AWPs in different sample years. Values on the horizontal axes represent the exponent of the logtransformed proportion of trees within each height class i where i = 0–2, 2–4, . . . , 18–20 m.

TABLE 1.

Response variable and model	AIC	F	df	P
Tree density, d				
Treatment	7770	0.139	1, 16.901	0.714
Year	7724	20.282	2, 222.526	<0.001
Distance	7706	1.201	5, 146.694	0.312
Year +	7693	18.839	2, 41.048	<0.001
Treatment(Year)		0.742	2, 29.750	0.485
Year +	7521	6.879	2, 369.460	<0.001
Distance(Year)		0.693	13, 205.298	0.769
Canopy cover, c				
Treatment	−145.974	0.079	1, 18.155	0.781
Year	−216.617	45.393	2, 233.815	<0.001
Distance	−134.866	1.642	5, 156.618	0.152
Year +	−210.881	20.509	2, 41.791	<0.001
Treatment(Year)		1.025	2, 29.961	0.371
Year +	−178.868	18.748	2, 321.571	<0.001
Distance(Year)		1.322	13, 222.432	0.201
Canopy volume, v				
Treatment	174.132	0.012	1, 15.004	0.915
Year	162.584	10.135	2, 250.802	<0.001
Distance	181.254	1.688	5, 169.370	0.140
Year +	168.775	3.123	2, 41.886	0.054
Treatment(Year)		0.022	2, 26.433	0.978
Year +	193.104	3.195	2, 339.431	0.042
Distance(Year)		0.936	13, 240.479	0.517
Tree height, h_s				
Treatment	13.670	8.803	1, 1.856	0.352
Year	22.545	0.140	2, 238.974	0.869
Distance	29.147	0.564	5, 168.764	0.728
Year +	22.764	0.525	2, 60.306	0.594
Treatment(Year)		3.347	2, 36.236	0.046
Year +	49.138	1.136	2, 327.279	0.322
Distance(Year)		1.562	13, 245.591	0.097
Tree height, h_l				
Treatment	384.354	5.387	1, 11.056	0.040
Year	150.363	175.753	2, 255.273	<0.001
Distance	396.699	0.906	5, 192.321	0.478
Year +	147.376	91.712	2, 85.967	<0.001
Treatment(Year)		5.041	2, 25.652	0.014
Year +	169.105	95.019	2, 297.481	<0.001
Distance(Year)		1.703	13, 272.881	0.060

Notes: The "df" column reports numerator degrees of freedom followed by denominator degrees of freedom. AIC is Akaike's Information Criterion, where a lower value indicates a better fitting model. Tree height: h_s, small (0.2–3.0 m); h_l, large (≥3.0 m).

TABLE 2.

Distance (m)	Treatment	Year	AWP			Nat.
			1997	2000	2008	2000
100	AWP	1997		−2.5138*	−8.7151***	
		2000			−5.6382***	
	Nat.	2000	8.349***	6.6064***	2.3784*	
		2008	9.0125***	7.0067***	3.5124**	0.538
500	AWP	1997		−2.1765*	−10.2633***	
		2000			−6.5695***	
	Nat.	2000	8.9597***	6.8263***	2.1923*	
		2008	4.8948***	2.8231**	−2.0993*	−3.8236***
1000	AWP	1997		0.944	−8.7502***	
		2000			−7.6461***	
	Nat.	2000	7.6571***	7.5455***	0.755	
		2008	5.4502***	5.3801***	−0.4073	−1.3499
2000	AWP	1997		−6.2353***	−6.4165***	
		2000			0.5589	
	Nat.	2000	7.6797***	2.8406**	3.5858**	
		2008	8.3047***	3.6213**	4.3237***	0.4314

Notes: Positive Z values indicate that the mean rank of the column variable is larger than that of its respective row variable. Key to abbreviations: AWP, artificial waterpoint; Nat., natural seasonal pan.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

PLATE 1.

A baobab (Adansonia digitata L.) that has been recently damaged by elephants. Anecdotal observations such as these have raised widespread concerns that increasing elephant numbers may have a negative impact on certain tree species in northern Botswana, Africa.

Photo credit: J. M. Kalwij.